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Long term resilience decline in plant ecosystems across the Danian Dan-C2 hyperthermal event, Boltysh crater, Ukraine.

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ABSTRACT

Mass balance calculations indicate that a massive amount of $\delta^{13}C$-depleted carbon was released into the early Danian atmosphere in volumes comparable with the younger Paleocene-Eocene thermal maximum (PETM). This Danian hyperthermal event (the Dan-C2) has been documented from the fill of the Boltysh meteorite crater, Ukraine. Palynofloras recovered from the Boltysh crater fill show a trend from mesic forest to savannah ecosystem dominance on a millennial scale across the hyperthermal inception with no abrupt compositional shift. This longer term trend is overprinted by moisture availability oscillations reflecting orbital forcing. Forcing is not directly tracked by the oscillations, which are composed of mesic forest and savannah palynofloras separated by rapid critical transitions. The absence of an ecological collapse at the Dan-C2 indicates that plant ecosystems experienced dominant forcing from orbital cyclicity, rather than a stochastic temperature rise.

INTRODUCTION

While gradual climate change dominates the long term geological record, short periods of rapid global warming on a deca-millennial scale (19k.y. Cui et al., 2010; 30k.y. Murphy et al., 2011), followed by slower recovery over tens to hundreds of thousands of years, have become the subject of intensive study. These hyperthermal events are commonly documented by pronounced negative carbon isotope excursions (CIE) caused by the addition of thousands of petagrams of ^{12}C-enriched carbon to the ocean-atmosphere system and thus record major short-term perturbations of the global carbon cycle. The Paleogene period includes several of these hyperthermal events, the Dan-C2 event at ca. 65.2 Ma (Quillévéré et al., 2008), the Latest Danian event at ca. 61.7 Ma (Westerhold et al., 2008; Bornemann et al., 2009), and the Danian-Selandian transition event at ca. 61 Ma (Speijer, 2003). However, the best documented hyperthermal remains the Paleocene-Eocene Thermal Maximum (PETM, see review by McInerney & Wing, 2011). The earliest of the Paleogene hyperthermals, the Dan-C2 event, has been documented in marine carbonate $\delta^{13}C$ and $\delta^{18}O$ records from the Atlantic (Quillévéré et al., 2008; Westerhold et al., 2011), western Tethys (Coccioni et al., 2010) and from the fill of the Boltysh meteorite crater, Ukraine (Gilmour et al. 2013, 2014). The marine Dan-C2 sections are well constrained by magnetostratigraphy and micropaleontology, being interpreted as post-dating the K/Pg boundary by less than 300 k.y. (Quillévéré et al., 2008).

Although the rate of climate change during these hyperthermal events is regarded as being an order of magnitude less than current anthropogenic climatic warming (Ridgwell & Schmidt, 2010; Haywood et al., 2011), paleontological records from these hyperthermals elucidate ecosystem responses to high levels of atmospheric CO_2. The majority of investigations of hyperthermal events have been conducted on marine sedimentary sequences, since they are more commonly preserved and held to be complete (e.g. Zachos et al., 2005). These examples document rapid environmental change at event initiation, often associated with biotic turnover and extinction of benthic organisms (Thomas, 1998; 2007). Studies of the terrestrial record of hyperthermal events are less common and apparently of

lower resolution than their marine counterparts (e.g. Hesslbo & Peinkowski, 2011: Wing & Currano, 2013). Accordingly, the rate of terrestrial environmental and ecosystem change, and its consequences are less well understood.

Plant macrofossil records across the PETM CIE demonstrate changes in floral dominance and diversity. Macrofloras from central North America show an incoming of dry subtropical taxa (Smith et al, 2007), with relatively rapid floral shifts across the hyperthermal inception (Wing et al., 2009). The PETM palynofloral record from this region is reported to lack clear indications of rapid compositional change, although these records are more detailed than those from other hyperthermal intervals (e.g. Riding et al., 2013). This paucity of data adds importance to the high resolution non-marine record of the Dan-C2 hyperthermal event in the fill of the Boltysh meteorite crater, Ukraine (Gilmour et al., 2013 and Figure 1). Mass balance calculations of a ~3‰ negative bulk organic $\delta^{13}C$ excursion (Gilmour et al., 2014), indicate that a massive amount of ^{12}C-enriched carbon was released into the early Danian atmosphere in volumes comparable with the PETM. In addition to the similarity of the Dan-C2 to the PETM, it is has a carbon-isotope record comparable to the geometry recorded at the Toarcian hyperthermal event (Kemp et al., 2005; Figure 2).

Because the Boltysh crater formed on the Proterozoic basement of the Ukrainian shield immediately prior to the K/Pg event (Kelley & Gurov 2002; Jolley et al., 2010), steady state, lacustrine conditions endured through the post-impact early Danian. Palynofloras derived from these lacustrine sediments show a series of compositional and diversity changes across the hyperthermal (Gilmour et al., 2013; 2014), but apparently lack any abrupt modification in composition at the CIE inception. Here, we examine the apparent disconnect between the palynological record of vegetation community change and the evidence for a geologically rapid period of climate warming.

Ecological Analysis

Palynofloral data derived from the analysis of 418 sediment samples at ~1m spacings taken from borehole 42/11 (Gilmour et al., 2013) were subjected to diversity and dominance

analysis and to ordination techniques to elucidate ecological trends. Detrended correspondence analysis was undertaken to identify major environmental trends within the palynofloras (using MVSP, Kovach, 2002 and PAST 3, Hammer et al., 2001). First, data reduction was undertaken to reduce 'noise', involving the removal of taxa which formed <2% of the total palynoflora. The reduced data set was then smoothed by transformation to square roots. A scatter plot of the first two DCA axes (27.8% cumulative variation) was used to identify taxa with similar spatial distributions (Figure 3). In contrast, the whole of the data set was utilised for indirect data analyses, results being smoothed using either Loess averaging or Box-Cox transformation (Hammer et al., 2001).

The botanical composition and stratigraphical distribution of the normalised palynofloral botanical affinity groups was calibrated to DCA sample axes (Figure 4), and utilised to define biomes. In the absence of previously defined earliest Paleocene biomes, these were constrained by taxonomic composition to Maastrichtian biomes (Figure 1 and Willis & McElwain, 2002). These are in turn derived from plant macrofossil data and are closely related to the palynofloristic provinces of Herngreen et al (1996).

Vegetation response to hyperthermal inception

Analysis of frequency distribution changes in botanical affinity groups (Figure 4) demonstrated that there was no abrupt compositional change at the CIE inception, isotope stage 2 (Gilmour et al., 2013). Instead, overall increased dominance of Normapolles and Juglandaceae from isotope stage 1 to the mid point of stage 2 was matched by a corresponding overall decline in mesic humid taxa (Pinaceae, Cupressaceae, Polypodiaceae, Cyathaceae, Fagaceae). These data indicate an extended period of plant community adaptation to warmer temperatures and decreased moisture availability. However, this long term trend is overprinted by shorter frequency compositional oscillations. Previously identified in the post K/Pg boundary - isotope stage 1 interval as moisture availability oscillations (MAO), these oscillations continue into the CIE and recovery stage (Jolley et al., 2013). MAO's are recorded by shifts from Pinaceae, Cyathaceae,

Polypodiaceae and Cupressaceae dominance, to late oscillation Normapolles, Juglandaceae and Platanaceae dominance over stratal thicknesses of 20-25m. These geologically rapid changes are interpreted by reference to botanical affinities, as representing shifts from warm temperate humid forest to a winterwet, or savannah-type open vegetation ecosystem. Over the period from the K/Pg boundary to mid isotope stage 2, there was a shift to increased moisture stress in the wet phase of each oscillation as a consequence of continued longer term warming. Evident as a decrease in frequency and diversity of humid temperate taxa (Figure 5), this trend is apparent in the Temperate:Winterwet ratio and from falling taxonomic distinctness. This last factor documents decreasing diversity of palynofloras at generic and family level, a response to increased stress from lower moisture availability. The consequence of the long term warming and drying climate and the overprinted MAO's, was a succession of local palynofloral extirpation (i.e. extinctions in the Boltysh record) events (Figure 5). These events are noticeable in the dryer, later phases of MAO's 2-6 (Figure 5) and mark the sequential extirpation of mesic taxa in response to increasing aridity.

Milankovitch-scale cyclicity in paleopaynological data has been reported from sediments as old as the early Mesozoic (e.g. Bonis et al., 2010). The Boltysh MAO oscillations are interpreted here as likely reflecting either 21ky (precession) or 41ky (obliquity) cycles (Jolley et al., 2013). Oscillations show an offset correlation (Figure 5) to cyclicity within the bulk $\delta^{13}C$ data, which have been in turn related to precession or obliquity cycles (Gilmour et al., 2013). Taken together with the relatively high paleolatitude of the Boltysh crater (~49°N, Figure 1), the wet phase – dry phase moisture fluctuation is compatible with variation in insolation over 41k.y. obliquity cycles.

Discussion

No Catastrophic Regime Change at the CIE

The palynological data derived from the 42/11 core samples shows that there was no catastrophic change in the plant ecosystem at the Dan-C2 CIE inception. A trend towards increased dominance of the winterwet biome palynofloras is recorded from the post K/Pg

boundary to within the Dan-C2 CIE, best reflected by the increased dominance of the Normapolles group. Despite this long term trend, there is change in plant ecosystem composition at the CIE inception, but it does not differ significantly from compositional shifts in the post K/Pg to Dan-C2 CIE interval. It is possible to derive two initial interpretations of the gradual response recorded in the palynological data across the Boltysh Dan-C2 CIE; that the early Danian hyperthermal had a gradual, rather than rapid onset, or that botanical factors control the large scale vegetation response to rapid climate change. Rapid temperature change >10°C over 20 k.y. (~5°C MAT, Wing & Currano, 2013) has been recorded at the inception of the PETM (Murphy et al., 2010), with these temperatures persisting for a further 80 k.y. – 113 k.y. (Murphy et al., 2010; McInerney & Wing, 2012). Comparable change is interpreted from the correlative $\delta^{18}O$ early Danian Dan-C2 event (Quillevere et al., 2008). These records negate any gradual warming hypothesis, although the magnitude and nature of the events remains a subject for debate (Sluijs & Dickens, 2012).

Because the Boltysh palynofloral record does not exhibit a critical ecosystem transition in response to rapid climate change at Dan-C2 inception, compositional shifts in the palynoflora have been investigated in detail. It is informative to compare the Boltysh record of long term change with the chronostratigraphy of the better documented PETM. A duration of 20 k.y.-30 k.y. for the Boltysh CIE onset and a subsequent 80 k.y. – 113 k.y. of persistent high temperatures (Figures 4, 5), would predict temperature declines from within MAO7 (assuming a ~41 k.y. MAO duration). Botanical composition (Figure 4), kurtosis and taxonomic distinctness (Figure 5), provide evidence of a warm-dry maximum during MAO7 – MAO8 at the peak $\delta^{13}C$ excursion. These oscillations are reflected in the lithology and wireline logs, intervals with lower moisture availability floras corresponding to outbuilding of lake-margin turbidite fans (Figure 5). This correlation likely reflects increased erosion in the catchment from mesic forest breakdown and its replacement by lower biomass, open savannah. This transition is comparable to responses to forest breakdown recorded in the Holocene of the Mediterranean (Sadori et al., 2011). Shifts between warm temperate and

winterwet biomes in the interval from the K/Pg boundary to within the lower part of the CIE indicate millennial vegetation community response to short-term forcing. In contrast, rapid warming at the CIE (isotope Stage 2) inception contributed to a buffered vegetation community response over 10's k.y.

What factors could have overridden rapid land surface temperature warming at the CIE, resulting in its uncoupling from vegetation community change? Part of the answer appears to lie in the position of the Boltysh impact crater in relation to biome boundaries (Figure 1). Vegetation records from other hyperthermals, in particular their palynofloras, show variability in frequency of pre-excursion taxa, but few inceptions or extirpations (Harrington & Jaramillio, 2007). The long term post K/Pg boundary to mid isotope stage 2 decline in humid temperate Cupressaceae and Pteridophyta (Figure 4) reflects a transition from warm temperate to winterwet biomes over ~300 k.y., marking the northward shift of the biome boundary. One potential reason for the uncoupling of rapidly increasing temperature from vegetation biome change is therefore inherent in the sensitivity of the site relative to the biome boundary. Putative locations to the north of present day Ukraine could record vegetation change wholly within the warm temperate biome.

Pre-adaptation

Similar records of repeated variation in temperature/moisture availability and $\delta^{13}C$ have been recorded as an interval of isotopic variation in the Toarcian hyperthermal (Hesselbo and Pienkowski, 2011), and in some PETM records (e.g. North Sea, Kender et al., 2012). In the Boltysh record, repeated switches between dominantly humid temperate and dominantly winterwet vegetation reflect ~160 k.y. of temperature and moisture availability fluctuation from the K/Pg boundary to within the CIE. Alternation between stable biome states would be expected to result in enhanced physiological adaptation within species and within floral communities. Repeated resurgences of humid temperate taxa leading up to the winterwet biome maxima supports an interpretation of preadaptation to moisture stress in regional vegetation dynamics. Reservoirs of physiologically adapted species and pre-adapted

communities could have existed in local enclaves around the island archipelago (see Daly & Jolley, 2015) site of Boltysh. However, a migrational connection to central Europe cannot be eliminated. Comparisons by the authors of the Boltysh palynofloras with other southern European Danian – Selandian palynofloral records failed to identify clear evidence for endemism (e.g. Kedves & Russel, 1982). Re-invasion of plants from potentially upland refugia into an open savannah-type ecosystem could have been relatively rapid. Significant Mediterranean Quaternary migrational lags occurred over 100's years (Ammann et al., 2013); in the k.y. context of the currently sampled Boltysh palynofloral record these would appear instantaneous. Within the Boltysh palynoflora, repeated minor extirpation events are recorded, particularly during the warm, dry phases of MAO2 and MAO4-MAO6 (Figure 5). This repeated elimination of sensitive warm temperate taxa would have resulted in increasing Normapolles dominance. As a consequence, palynofloras recovered from MAO7 - MAO8 represent the period of optimum community adaptation to the winterwet regime.

Alternative states

The lack of significant changes in the palynological records of PETM sites in Wyoming and Alabama have previously been attributed to floral intertia (Wing et al., 2003, 2009). While this may have contributed to vegetation conservatism during early Danian humid climate phases in the Boltysh record, it would have been of lesser significance in the lower biomass winterwet vegetation community (Bailey, 2014). In contrast to inertia, the Boltysh record shows repeated, rapid alternations between parallel stable biomes in the interval prior to and during the Dan C2 CIE (Figure 5). Intuitively, an extrinsically forced event such as Dan-C2, would have instigated a critical transition from mesic temperate forest into a winterwet stable state (Scheffer et al., 2001; Veraart et al., 2012; van Nes & Scheffer 2007). Such a critical transition is not observed in the Boltysh data, which shows the continuation of MAO's, albeit at decreasing amplitude (Figure 5). Post K/Pg boundary Milankovitch-mediated oscillations in vegetation ecosystem composition could be expected to track multi-dimensional climate forcing. Simple tracking of climatic warming from cool/wet to warm/dry orbital-forced cycles would have yielded a sinusoidal response in mesic and savannah-type vegetation

communities. This is not the response observed in the Boltysh record. Both mesic forest and savannah biomes appear stable during respective cool and wet, to warm and dry phases of each MAO, reflecting resilience within each biome to orbitally-forced climate change (see examples in Scheffer et al, 2001). Transition between these stable mesic forest and savannah states was rapid, being completed within ~8% of the total 20m-25m MAO strata thickness (a transition duration of approximately 3 k.y. assuming 41 k.y.obliquity cycles).

Because of the rapidity of the transitions between mesic and winterwet biomes, and their repetition at declining amplitude, they can be compared to 'flickering' responses in present day biological populations or systems, prior to regime shifts (Dakos et al, 2013, 2015). However, the current Boltysh record displays this putative flickering over 10's k.y.s, an order of magnitude greater than flickering of Dansgaard – Oeschger events in the last glacial period (Dakos et al., 2013), and significantly longer than the years duration of other Holocene records (e.g. Wang et al., 2012). Because of this long duration event frequency, the rapid shifts between mesic and winterwet biomes are interpreted here as being comparable to critical transitions leading to regime (biome) shifts. Their pattern of biome stability followed by rapid transition to an alternative stable state (biome) follows patterns modelled from slow environmental change towards a tipping point (Dakos et al, 2015). In the Boltysh ecosystem the tipping point marks the time at which winterwet or mesic forest biome resilience was overcome by climate forcing. Following this interpretation, flickering would be expected occur in plant ecosystems prior to these critical transitions in late mesic forest and winterwet biome states. However, the shorter time frequency of such flickering is not reliably observed in the current Boltysh data set, remaining below the resolution of 1m spaced samples.

Conclusions

From the palynological evidence recovered from a sequence of 1m spaced samples in Boltysh borehole 42/11, it is clear that vegetation response to rapid climate change at the CIE inception was long duration transformation, not regime change of ecosystems. The long

term trend demonstrates the overall decrease in moisture availability prior to, and subsequent to the CIE inception. This is superimposed onto a record of shorter duration shifts between stable warm mesic forest and winterwet biome dominance. Repeated critical transitions between these mesic and winterwet plant biome states occurred in the pre-CIE and CIE intervals. Repeated rapid switching of organisms, or ecosystems between stable states has been termed flickering in comparative modern ecological systems (Wang et al., 2012). Although the Boltysh record could be viewed as demonstrating long periodicity flickering prior to the Dan-C2 hyperthermal event, this is not supported by the absence of regime change at the CIE. Stronger candidates for critical shifts are recorded at the boundaries between stable biomes, occurring between MAO's at winterwet – mesic forest biome shift and within MAO's at mesic forest – winterwet shift. The duration and repetition of these MAO's indicates that they record plant ecosystem responses to orbital forcing. The presence of stable ecosystems separated by critical transitions indicates that plant community pre-adaptation of mesic species played a significant role in building mesic forest resilience. Contributory factors in this pre-adaptation would have been repeated migrations, floral intertia within mesic forests and individual taxon ecological tolerances which could have overlapped between temperate and winterwet biome states.

The magnitude of shifts between biome states became suppressed after the CIE inception, reflecting greater resilience in the winterwet biome with increased temperature/low moisture following the CIE inception. The Boltysh record indicates that Milankovitch-mediated cyclicity (likely obliquity) operated stronger forcing on plant ecosystems than the Dan-C2 hyperthermal. Particular to the Boltysh record may be the coincidence of the cooler, high moisture availability (mesic forest) phase of MAO5 with the rapid increase in temperature implied by the negative CIE inception. Such superposition could have mitigated rapid warming, lessening the effect on regional vegetation. However, this would potentially be succeeded by amplification of the continuing δ^{13}C-depleted carbon excursion in the later, warmer and dryer phase of MAO5. This response is not evident.

The current analysis of the Boltysh palynofloral record has highlighted areas of uncertainty which invites future investigation. Firstly, it is desirable to examine other hyperthermal records for pre-CIE (isotope stage 1 and earlier) variability in the $\delta^{13}C$ record. In several terrestrial hyperthermal records, sampling of the interval prior to the hyperthermal is absent or sporadic, preventing comparison. It is therefore possible that vegetation community and climate instability in the period between the K/Pg and CIE inception may be a consequence of post K/Pg ecosystem instability. Until the pre-CIE interval of other hyperthermal is investigated in detail it is not possible to differentiate between instability inherent in the approach to a hyperthermal, or perturbation following the K/Pg event.

From the Boltysh record, it is evident that vegetation change does not simply mirror potential forcing from either orbital cyclicity or stochastic global temperature change. This observation is practical because of the high deposition rate, steady state depositional system of the Botlysh crater. It emphasises how conceptions of rapid change in climate proxies in the geological record are likely distorted by the fidelity of individual rock records and the physical limitations of sampling.

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Figure 1. Location map of the Boltysh impact crater, showing the extent of Maastrichtian biomes in the northern hemisphere (after Willis & McElwain, 2002).

Figure 2. Comparison of bulk omδ^{13}C from three hyperthermal events. The complete record for each individual CIE was scaled proportionally, giving a common alignment of the inception and termination of the individual CIE's. There is evident similarity between the Toarcian CIE, Yorkshire, UK (Kemp et al., 2005) and the early Danian Boltysh record (Gilmour et al., 2013). A less clear comparison is made to the PETM at Polecat Bench, Wyoming (Wing et al., 2005). This terrestrial record may differ because of the greater sample spacing. In contrast, the marine PETM record of ODP 1263 (Murphy et al., 2010) displays a smoothed trend comparable to that seen in both the Toarcian and Danian events.

Figure 3. Plot of first two axes of detrended correspondence analysis of the Boltysh palynofloras recovered from 42/11. Many of the taxa which comprise the warmest communities belong to the extinct polyphyletic Normapolles group which lack a detailed knowledge of their botanical affinity (Daly & Jolley, 2015). Botanical affinities of the taxa indicate that Axis 1 reflects temperature/biome, while axis 2 reflects moisture availability.

Figure 4. Stratigraphical plot of the frequency of taxa recorded in the Boltysh 42/11 borehole. The taxa are shown as percentages of the whole pollen/spore flora. The first two axes from the DCA analysis of the same data set are plotted; Axis 1 reflects biome or temperature, axis 2 reflects moisture availability. Heavy dashed horizontal lines are used for major biome changes which are identified with reference to the DCA axes and the taxa frequency plots. Light dashed lines identify events of lesser significance. Dashed line 'a' marks the transition from warm temperate to winterwet, coinciding with the CIE inception. Light dashed line 'b' marks the winterwet biome maximum. Light dashed line 'c' marks a significant change in the crater hydrological system, and is coincident with the re-appearance of abundant *Botryococcus braunii* (Chlorphyceae; see Gilmour et al., 2014). Dashed line 'd' marks the onset of warm temperate biome which shows a transition into a cool temperate biome at line 'e'. All data is plotted alongside the bulk omδ^{13}C record (Gilmour et al., 2013).

Figure 5. Lithological and statistical record of the 42/11 borehole, showing wireline logs and indirect indicators derived from palynology data. The GR (gamma ray log) and GGR (gamma – gamma logs) show natural gamma radiation and formation density. Note the appearance of reworked ejecta below 560m as high GR log values. The build-out of crater margin fans during the winterwet phase of MAO3 and the decline in grain size of clastic material during the main CIE is also evident from the GR log. The warm temperate – winterwet ratio plot is labelled to show MAO's 1-11, compositional change in the biomes above this requiring different ratio plots for the late-recovery and post-recovery periods. It is noteworthy that following the Dan-C2 CIE inception, the frequency of MAO's remains constant, but the amplitude decreases (Standard deviation of temperate:winterwet 571m- 486m, 4.98; 360m-485m, 0.34). This reflects the overall dominance of the winterwet biome following the CIE. All other indirect indicators derived from the palynological data are plotted as smoothed lines (S) using Loess average smoothing to highlight longer term trends. Diversity in the pollen and spore palynoflora is measured by Menhinick's richness index which calculated the ratio of the number of taxa to the square root of sample size. Along with Brillouin's diversity index these are used to reduce bias introduced by lithological variation, and closely follow Species Richness. Evenness compares the actual, to the maximum possible diversities. Floras with the greatest evenness occur during the CIE, with subsequent decrease and wide fluctuations in the recovery interval where single taxa can dominate assemblages. In contrast the emphasis placed on the single taxon records, Distinctness (Taxonomic Distinctness, Clarke & Warwick, 1999) utilises the taxonomic hierarchical relationship of the palynofloral components. This index highlights the possibility that recovery from the maxima of the CIE, which begins within Stage 2 (see Brillouin's Index and Kurtosis) is not paralleled by a taxonomic recovery into Stages 3 and 4. . All data is plotted alongside the bulk om$\delta^{13}C$ record and the cyclicity present in these data (Gilmour et al., 2013, 2014).